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AN EXPERIMENTAL STUDY OF THE FOOD INTAKE OF THE OYSTERCATCHER *HAEMATOPUS OSTRALEGUS* L. IN CAPTIVITY DURING THE SUMMER

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CONTENTS

1. INTRODUCTION

The feeding ecology of the Oystercatcher has been studied bij several authors (Dewar 1908; Drinnan 1957, 1958a and b; Davidson 1967; Heppleston 1971; Dare & Mercer 1973; Hulscher, in preparation). One aspect of these studies has been an attempt to measure the food intake quantitatively. However, despite the number of studies the daily food intake in the field could as yet not be adequately determined because of the difficulties in determining satisfactorily food intake at night (Drinnan 1958b). In captivity measurements of food intake during the day and during the night can be checked under controlled conditions. Moreover, close observations on the behaviour of birds while handling prey can also be carried out (Hulscher, in preparation).

The following aspects of feeding ecology are treated in this study:

1. food intake under tidal and non-tidal feeding schedules,
2. food intake in daylight and in darkness,
3. daily food intake with different prey species *(Cardium* and *Mytilus),*
4. daily food intake in relation to body-size.

2. TECHNIQUE

This study was carried out on Schiermonnikoog, one of the Frisian islands in the Dutch Waddensea. During the breeding seasons of 1964 to 1967 inclusive several Oystercatchers were caught on their nests, with a spring trap operated from a hide. After clipping the primaries of one wing the birds were kept in cages on a grassfield, 50 m from the field station. The cages were made of chicken wire, 400 x 400 x 75 cm, without a roof. The walls were lined on the inside with semi-transparent cloth in order to prevent the birds from sticking their bill through the meshes and wounding themselves. A screen in front of the cages reduced disturbance from people moving about. During the first few days of captivity Cockles *Cardium edule* and Mussels *Mytilus edulis,* were presented in the opened state (if placed a few seconds in boiling water shellfish readily gape).
Gradually these pre-treated shellfish were replaced by live intact shellfish. After a week or so most birds were able to feed solely on intact shellfish. Natural terrestrial food was only occasionally seen to be taken and only during the first days of captivity; for present purposes it can be neglected quantitatively. After an initial loss body-weight stabilized at about 80-94% of the level at capture. During the feeding experiments the shells cleaned by the birds were collected, counted and measured. The amount of flesh consumed was calculated in millilitres fresh weight from curves relating shell-length and flesh content (cf. Drinnan 1957, 1958a). Every time a fresh batch of Mussels was collected a new curve was computed. The body-weights of the birds were determined with a spring balance.

3. FEEDING PATTERN UNDER NON-TIDAL AND TIDAL SCHEDULES

3.1. SCHEDULES OF FOOD PRESENTATION

Outside the breeding season the feeding pattern of Oystercatchers in the Waddensea is dependent on the tidal cycle, feeding only being possible when the tide is out during the day as well as during the night. The majority of the Oystercatchers feed 5 hours per tide, corresponding with the emersion period of their main feeding grounds: Musselbeds and lower-level Cocklebeds. Some birds feed at the higher levels in the intertidal zone where they can stay at most 7½ hours per tide. During the breeding season many pairs supplement their marine diet with terrestrial food found in their nesting territories. These birds theoretically can feed 24 hours per day. Failed breeders, subadults and juvenile birds feed in concordance with the tidal cycle during the breeding season.
In the experiments with captive birds I tried to realize the feeding schedules as experienced by the Oystercatchers in the field. The birds were either allowed to feed 24 hours per day (non-tidal schedule), or during two periods of 5 or of 7½ hours, one around midday and one around midnight (tidal schedules).

The following test-series were carried out:

Series 1, non-tidal schedule:
food available 24 hours per day, emptied shells collected once per day at 18.00 hrs, total duration of test-series 11-15 days; this series was performed by the birds nrs. 65-1, 65-2 and 65-3.

Series 2, tidal schedule:
food available from 10.00-15.00 and 22.00-03.00 hrs, shells collected after each feeding period at 15.00 and 03.00 hrs, total duration 25-29 days; this series was performed by the nrs. 65-1, 65-2 and 65-3.

Series 3, non-tidal schedule:
food available 24 hours per day, shells collected at 03.30 (04.00), 10.00 (09.00), 15.00 and 21.30 (21.00) hrs, total duration 15-17 days; this series was performed by the nrs. 65-1, 65-2, 65-3, 65-4, 65-5 and 64-1.

Series 4, tidal schedule:
food available from 08.45-16.15 and 20.45-04.15 hrs, shells collected at 16.15 and 04.15, total duration 22 days; this series was performed by nr. 65-3.

Test-series 1 and 2 were not only set up to study the feeding pattern under tidal and non-tidal feeding schedules but also to study size preference of the Oystercatcher with Mussels (Hulscher, in preparation). Therefore, the size distribution of the Mussels offered to and consumed by the birds differed within and between test-series 1-4 (cf. Table 3). The size distribution of the

Mussels offered during the daylight and during the dark feeding period of a particular day were always the same. Food was always available in excess.

3.2. RESULTS FOR THE NON-TIDAL SCHEDULE

During test-series 1 the emptied shells were collected once a day. Therefore, this series informs us on the mean feeding rate per 24 hours, but not on the feeding rate during different periods of the daily cycle. The latter information is given by test-series 3 because in this series emptied shells were collected 4 times per 24 hours. The results of test-series 3 will be given first. (The results of test-series 1 are discussed on page 000).

Series 3 was performed by the nrs. 65-1 to 5 from 15-29 July 1965, the night period (from dusk to dawn) lasting from 21.30-03.30 hrs, and by nr. 64-1 from 25 Aug.-10 Sept. 1964, the night period lasting from 21.00-04.00 hrs. The results are depicted in Fig. 1A. The feeding rate is expressed as the mean volume of flesh eaten per hour (ml/h).

For each of the six birds it was tested (analysis of variance) over the total duration of the test-series whether the feeding rate during the four periods of the daily cycle deviated significantly from the mean rate for the total 24-hour period. This was the case for 5 birds ($p < 0.05$), but not for nr. 65-2 ($p > 0.05$). The patterns of the feeding rate over the daily cycle differed markedly between the individuals. For the nrs. 65-1, 65-2 and 65-3 the rate of intake was lowest during the midday period and highest during the late afternoon, for the nrs. 65-4 and 65-5 feeding rate was highest during the late afternoon but lowest at night, whereas for nr. 64-1 the lowest rate was at night, the highest during the early morning.

The patterns of the feeding rate of the nrs. 65-1, 65-2 and 65-3, and also

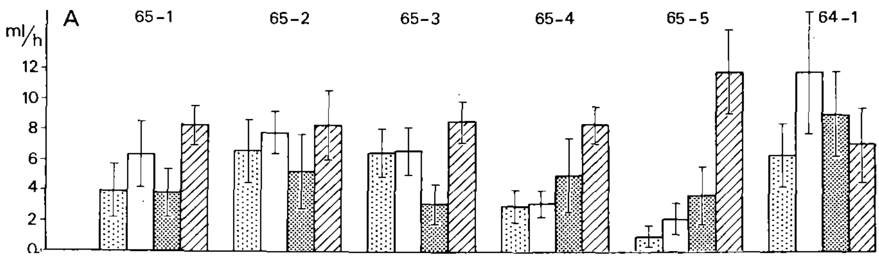

Fig. 1A. Mean feeding rate (ml fresh Mussel flesh/h) of 6 Oystercatchers during four periods of the daily cycle when food is available 24 hours (non-tidal schedule) averaged over 15 days (nrs. 65–1 to 5), and over 17 days (nr. 64–2); feeding periods:

	for nrs. 65–1 to 5	for nr. 64–1
night	21.30–03.30;	21.00–04.00
early morning	03.30–10.00;	04.00–09.00
midday	10.00–15.00;	09.00–15.00
late afternoon	15.00–21.30;	15.00–21.00

vertical bars indicate one standard deviation.

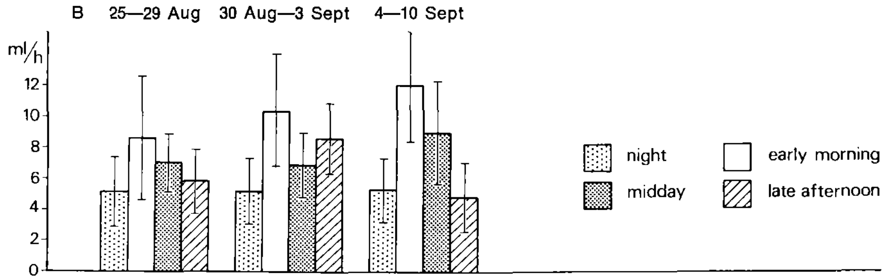

Fig. 1B. Feeding rate (ml fresh Mussel flesh/h) of nr. 64–1 during four periods of the daily cycle when food is available 24 hours (non-tidal schedule) during 3 sub-periods:
25–29 Aug. with clear moonlit nights
30 Aug.–3 Sept. with cloudy nights and a waning moon
4–10 Sept. with very dark moonless nights;
feeding periods as indicated at fig. 1A under nr. 64–1;
vertical bars indicate one standard deviation.

those of the nrs. 65-4 and 65-5 correspond to each other. The causes for this are not understood, but the birds may have influenced each other, visual isolation being incomplete. The birds nr. 65-1 to 3 were housed adjacent to one another, nrs. 65-4 and 5 also, but separate from the rest.

For nr. 64-1 the total length of test-series 3 was devided in 3 sub-periods: 25-29 Aug. with clear moonlit nights (full moon at 23 Aug.), 30 Aug.-3 Sept. with cloudy nights and a waning moon, and 4-10 Sept. with very dark moonless nights. The results of the mean feeding rate during the four periods of the daily cycle are depicted in Fig. 1B. Obviously the rate of intake during darkness did not change with different light conditions at night.

3.3. RESULTS FOR THE TIDAL SCHEDULE

Test-series 2 was performed by the birds nrs. 65-1, 65-2 and 65-3 from 14 June-5 July 1965, series 4, by bird nr. 65-3 only, from 15 Aug.-5 Sept. 1965. Table 1 summarizes the results. Feeding rate is expressed as the

Table 1. Mean food intake (ml fresh Mussel flesh) during a feeding session of 5 hours (series 2) or 7½ hours (series 4) around midday and around midnight (tidal schedule).

bird nr.	series nr.	days	day 10.00–15.00 (08.45–16.15)*		night 22.00–03.00 (20.45–04.15)*		F	p**
			ml	s.d.	ml	s.d.		
65–1	2	29	47.1	± 30.4	86.9	± 34.2	> 13	< 0.01
65–2	2	29	78.0	± 27.4	92.1	± 42.9	2.25	> 0.20
65–3	2	25	43.7	± 30.3	75.4	± 30.1	13.75	< 0.01
65–3	4	22	48.6	± 20.4	52.7	± 25.4	0.35	> 0.50

* during series 4 only

** significance of difference according to analysis of variance

Table 2. Feeding rates (ml fresh Mussel flesh/h) in daylight and darkness, under nontidal and tidal schedules

	non-tidal					tidal			
bird nr.	series nr.	days	midday period 10.00–15.00 ml/h (%)	total daylight period 03.30–21.30 ml/h (%)	night period 21.30–03.30 ml/h (%)	series nr.	days	midday period 10.00–15.00 (08.45–16.15)* ml/h (%)	night period 22.00–03.00 (20.45–04.15)* ml/h (%)
65–1	3	15	3.68 (100)	6.04 (163)	3.76 (102)	2	29	9.42 (100)	17.38 (184)
65–2	3	15	5.00 (100)	7.27 (146)	6.35 (127)	2	29	15.60 (100)	18.42 (118)
65–3	3	15	3.03 (100)	5.89 (194)	6.21 (205)	2	25	8.74 (100)	15.08 (172)
65–3						4	22	9.72 (100)	10.54 (108)

* during series 4

amount of flesh (ml) eaten per feeding period of 5 (7½) hours. For all three birds the feeding rate at night was higher than during the day (not significantly for the nrs. 65-2 and 65-3, series 4). The marked difference in the ratio of the day and night feeding rates of bird nr. 65-3 in test-series 2 and 4 can not be satisfactorily explained.

3.4. COMPARISON OF RATE OF INTAKE DURING NIGHT AND DAYLIGHT PERIODS

The feeding rates of the birds nrs. 65-1, 65-2 and 65-3 in daylight and in darkness can be compared under non-tidal (series 3) and tidal (series 2 + 4) schedules (Table 2). The feeding rate at the night period under non-tidal schedules as compared to that during the total daylight period was lower (but not significantly) for the birds nrs. 65-1 (Student: $p > 0.05$) and 65-2 ($p > 0.1$) and slightly higher for nr. 65-3 ($p > 0.2$). The combined results of the three birds show a ratio between the night and total daylight period of 0.86 : 1. If the feeding rate in the night period, however, is compared to that in the midday period all three birds ate at a higher rate around midnight (significant only for nr. 65-3: $p < 0.01$). The combined results for the three birds show a ratio of 1.45 : 1 for the night compared to the midday period. The latter ratio corresponds to the feeding data under tidal schedules. Here too, the combined results of the three birds show a ratio of 1.45 : 1 for the periods around midnight and midday. It is a plausible supposition that the

Table 3. Influence of Mussel size upon daily food intake

bird nr.	series nr.	feeding period h/day	number of Mussels consumed per test	days	ml/day	s.d.	F	p
65–1	1	24	1050 s + 707 m	13	141.9	± 65.9	0.24	> 0.50
	3		1220 stand.pop. B	15	132.6	± 30.7		
	2	2 × 5	1060 s + 237 b	11	135.9	± 76.0		
	2		267 m + 113 b	7	109.9	± 25.4	0.83	> 0.50
	2		775 stand.pop. A	7	145.0	± 16.0		
65–2	1	24	803 s + 517 m	7	196.7	± 31.2		
	1		978 s + 119 b	6	160.3	± 42.1	1.59	> 0.20
	3		1554 stand.pop. B	15	169.0	± 42.6		
	2	2 × 5	859 m + 275 b	13	168.5	± 45.1		
	2		556 s + 513 m + 130 b	9	177.3	± 11.1	1.14	> 0.50
	2		785 stand.pop. A	7	145.7	± 59.8		
65–3	1	24	505 m + 143 b	9	136.2	± 40.8	0.21	> 0.50
	3		1314 stand.pop. B	15	142.8	± 30.1		
	2	2 × 5	736 s + 569 m	10	140.9	± 62.2		
	2		647 s + 274 b	12	109.3	± 35.7	2.16	> 0.20
	2		190 stand.pop. A	3	82.3	± 30.9		

s = small Mussels	:	25–37, mean 32 mm, mean flesh content	0.71 ml/spec.
m = medium-sized	:	38–49, „ 43 mm, „ „ „	1.56 ml/spec.
b = big	:	50–70, „ 57 mm, „ „ „	3.10 ml/spec.
standard pop. A	:	23–58, „ 38 mm, „ „ „	1.30 ml/spec.
standard pop. B	:	25–55, „ 40 mm, „ „ „	1.60 ml/spec.

nightly feeding rates were higher because the daylight feeding period always coincided with the midday period, when the feeding rate tends to be low.

3.5. INFLUENCE OF MUSSEL SIZE UPON FOOD INTAKE

Opening large Mussels may require more energy than opening small ones; on the other hand large Mussels yield more flesh than small ones. The sizes of the Mussels the experimental birds were feeding upon during the different test-series were not the same. Therefore, before we are able to compare the daily food intake under different feeding schedules the influence of Mussel size upon food intake has to be investigated.

The results (Table 3) show no significant difference in daily food intake if Mussels of different size classes were consumed (data from each bird considered separately). We therefore may conclude that under the experimental conditions involved the size of the Mussel presented (25-70 mm) did not influence the daily food intake. It should be noted that the range presented is within the range normally taken by Oystercatchers.

3.6. DAILY FOOD INTAKE UNDER THE VARIOUS FEEDING SCHEDULES

Without having to take into account the sizes of the Mussels the birds were feeding upon we can now compare the daily food intake under different time schedules. In Table 4 the results of the birds nrs. 65-1, 65-2 and 65-3 are summarized. For each of the three birds no significant differences were found in daily food intake between the series. We may conclude that with a time budget of 2 x 5 (7½) hours per day, corresponding with the feeding schedule in the field under tidal conditions, the birds managed the same total intake as under conditions of continual presence of food.

4. FLUCTUATION OF THE DAILY FOOD INTAKE AND COMPARISON OF FOOD INTAKE WITH *CARDIUM* AND *MYTILUS*

Data of the birds nrs. 66-1, 66-2 and 66-3 on food intake over a considerable number of consecutive days give an insight in the fluctuations of the

Table 4. Daily food intake (ml fresh Mussel flesh) when feeding under different schedules

	hours feeding per dag													
	24 series 1			2 × 5 series 2			24 series 3			2 × 7½ series 4				
bird nr.	ml	s.d.	days	ml	s.d.	days	ml	s.d.	days	ml	s.d.	days	F	p*
65–1	141.9	± 65.9	13	133.8	± 50.4	29	132.6	± 30.7	15	—	—	—	0.15	> 0.50
65–2	183.1	± 37.8	15	165.7	± 42.7	29	169.0	± 42.6	15	—	—	—	0.89	> 0.50
65–3	145.6	± 46.8	11	118.7	± 50.3	25	142.8	± 30.1	15	122.8	± 25.3	14	1.78	> 0.20

* significance of differences according to analysis of variance

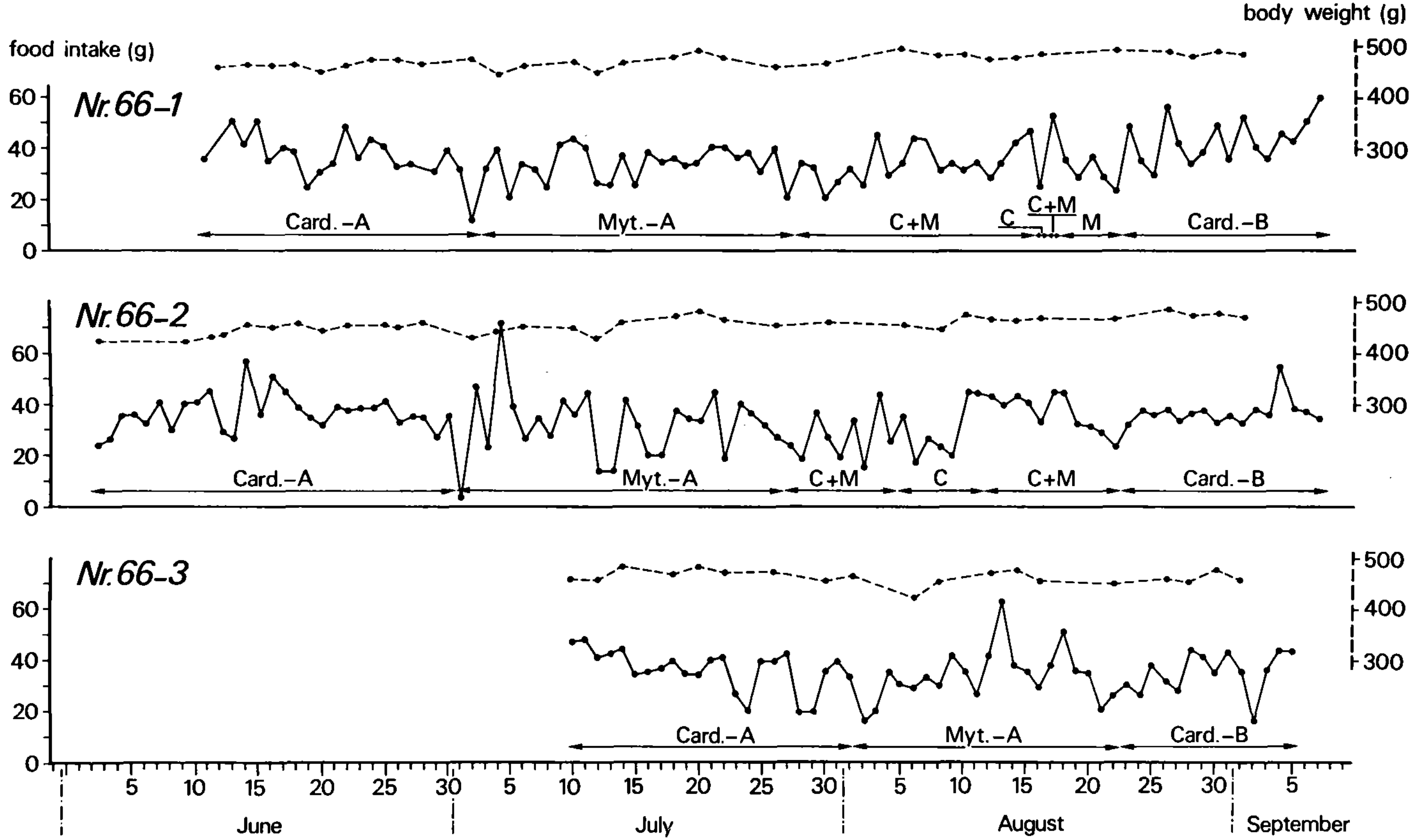

Fig. 2. Daily food intake (grams flesh, ash-free dry weight; drawn line) and body weight (broken line) of three captive Oystercatchers when feeding upon *Cardium* or *Mytilus* or upon a mixture of these two prey species. The letters A and B denote the first and second experimental sessions.

daily intake (Fig. 2). The birds were either feeding on one prey, either Cockles or Mussels, or on a mixture of both. Food was always available in excess during 24 hours per day. The Cockles consumed ranged in size from 23-37 mm (mean 30-31 mm), the Mussels from 27-64 mm (mean 46-47 mm). There is little variation in caloric value per gram ash-free dry weight of bivalve flesh, either between species or for one species between different seasons of the year. Swennen (pers. comm.) found for *Cardium* and *Mytilus* sampled from the Dutch Waddensea values varying between 5.1 and 5.2 kcal per gram, irrespective of size and season. Heppleston (1971) reports for *Mytilus* in April a value of 5.385 kcal per gram. Corresponding values are found by Hughes (1970) for *Scrobicularia plana,* varying from 4.890-5.261 kcal per gram over a period of 15 months. Thus one can compare nutritive values between bivalves in grams ash-free dry weight directly. The specific weight of fresh Cockle and Mussel flesh was determined after drying a known volume of wet flesh on the outside with filterpaper, and the percentage total dry weight after drying the flesh during 2 × 24 hours at 102°C till constant weight. The percentage ash-free dry weight was calculated after having determined the ash content by heating the dry flesh during 2 hours at 400°C. The birds were weighed at irregular intervals of 2 to 5 days.

The food intake (Fig. 2) varied between wide limits from day to day for all three birds (standard deviations 24-29% of the mean); no particular time pattern was evident. Many, but not all, of the largest fluctuations occurred in the first few days after the birds were put on another prey.

The body-weight of the three birds varied between rather narrow limits (standard deviations 3-4% of the mean). Short-term changes in body-weight as may be expected to result from inconstant food intake do not appear from our data, because body-weight was not determined frequently enough. Probably most of the variations in body-weight were correlated with the amount of food the birds had eaten just before being weighed, the mean daily food intake (fresh weight) being 40% of the mean body-weight.

Table 5 summarizes data on food intake when either *Cardium* or *Mytilus* was offered. Only periods of a sufficient length are compared: two *Cardium* periods (Card. -A and Card. -B) and one *Mytilus* period (Myt. -A, cf. Fig. 2). Food intake was measured in millilitres fresh (column 5) and in grams ash-free dry weight (column 6).

In all cases the birds consumed significantly more fresh *Cardium* flesh than *Mytilus* flesh, whereas the intake during the periods Card. -A and Card. -B was not different. Expressed in grams ash-free dry weight in all cases but one (nr. 66-1, Card. -B versus Myt. -A), the birds consumed no significantly different quantities of both prey species. The intake of nr. 66-1 during period Card. -B was higher than during period Card.-A.

Table 5. Comparison of food intake with *Cardium* and *Mytilus*

1 bird nr.	2	3 feeding period	4 days	5 volume fresh ml ± s.d.	6 dry weight ash-free g ± s.d.	7 body-weight g ± s.d.	8 number of weighings (n)
66-1	11 June–3 July	Card.-A	23	197 ± 46.6	36.3 ± 8.6	462 ± 11.1	11
	4–27 July	Myt.-A	24	151 ± 31.3	34.0 ± 7.1	467 ± 15.5	9
	23 Aug.–7 Sept.	Card.-B	16	218 ± 44.5	43.3 ± 8.7	486 ± 4.4	4
66-2	2–30 June	Card.-A	29	197 ± 39.0	36.3 ± 7.2	445 ± 14.2	12
	1–27 July	Myt.-A	27	141 ± 59.4	31.8 ± 13.4	452 ± 18.0	10
	23 Aug.–7 Sept.	Card.-B	16	181 ± 29.5	36.2 ± 25.8	477 ± 7.1	4
66-3	11 July–2 Aug.	Card.-A	23	189 ± 41.9	36.9 ± 8.2	472 ± 10.4	8
	3–23 Aug.	Myt.-A	21	148 ± 41.3	33.9 ± 9.5	459 ± 19.6	6
	24 Aug.–6 Sept.	Card.-B	14	184 ± 42.8	35.4 ± 8.2	464 ± 9.9	4

categories tested	feeding periods compared	66–1 t	66–1 p*	66–2 t	66–2 p	66–3 t	66–3 p
volume fresh (ml)	Card.-A × Myt.-A	3.977	< 0.001	4.213	< 0.001	3.289	< 0.001
„ „	Card.-B × Myt.-A	5.604	< 0.001	2.439	< 0.02	2.469	< 0.02
„ „	Card.-A × Card.-B	1.423	> 0.10	1.466	> 0.10	0.393	> 0.50
dry weight ash-free (g)	Card.-A × Myt.-A	0.997	> 0.20	1.580	> 0.10	1.094	> 0.20
„ „ „	Card.-B × Myt.-A	3.723	< 0.001	1.237	> 0.10	0.465	> 0.50
„ „ „	Card.-A × Card.-B	2.498	< 0.02	0.059	> 0.50	0.528	> 0.50
body-weight (g)	Card.-A × Myt.-A	0.579	> 0.50	0.787	> 0.20	1.738	> 0.10

* significance of difference according Student-test

No significant differences in the average body-weights during the feeding periods Card. -A and Myt. -A were found for any of the three birds. The number of weighings during the Card. -B period is too small to make comparisons with the other feeding periods possible.

These experiments permit the conclusion that irrespective of the short-time fluctuations the birds take the same amount of food (ash-free dry weight) per day while keeping a roughly constant body-weight, independently of whether they are feeding on *Mytilus* or on *Cardium*.

5. FOOD INTAKE AND BODY-WEIGHT

Table 6 summarizes the data available on the mean daily food intake with Cockle and/or Mussel flesh in summer and the weight (at capture and in captivity) of nine individual birds. The sex of 4 birds was determined by dissection when they later on died. Of the other birds 66-1 was qualified as a ♂ because it was paired to a sexed ♀, the nrs. 65-4 and 65-5 formed a pair, 65-5 with the longest bill probably was the female; the nrs. 64-1 and 64-2 also formed a pair, the bill of 64-1 was not measured, but the very long bill of nr. 64-2 suggests this one being the female.

Differences between individuals in the mean daily food intake were large,

Table 6. Mean daily food intake of nine Oystercatchers

bird nr.	days	prey species	fresh weight g	s.d.	fresh volume ml	s.d.	dry weight ash-included g	s.d.	dry weight ash-free g	s.d.	body-weight at capture g	body-weight in captivity (mean) g	number of weighings	bill-length mm	sex
64–1	48	Mytilus	152		145		26.6		24.0		503	442	3	?	♂
64–2	78	Mytilus	176		169		26.0		23.5		503	473	4	76.6	♀
65–1	57	Mytilus	144	± 52.5	134	± 49.5	29.6	± 10.6	26.8	± 9.6	483	453	3	72.9	♂ *
65–3	73	Mytilus	130	± 48.0	123	± 45.3	28.8	± 10.4	25.8	± 9.4	520	453	4	67.0	♂ *
65–4	46	Mytilus	117	± 49.4	110	± 46.5	28.8	± 12.1	26.1	± 10.9	513	469	4	71.6	♂
65–5	46	Mytilus	120	± 58.0	113	± 54.7	29.4	± 13.9	26.9	± 13.0	545	461	4	79.4	♀
66–1	89	Myt. + Card.	187	± 51.0	176	± 47.9	41.8	± 10.2	36.3	± 8.7	556	473	31	70.9	♂
66–2	98	Myt. + Card.	177	± 55.0	166	± 51.6	39.2	± 11.6	34.0	± 9.9	570	456	33	71.3	♀ *
66–3	58	Myt. + Card.	184	± 48.4	173	± 45.4	40.6	± 10.0	35.5	± 8.6	527	466	18	80.5	♀ *

* sexed by dissection

varying between 23.5 - 36.3 g ash-free dry weight per day. Data on food intake of the same birds in different years, however, showed little variation. For instance, the intake of nr. 66-1 with Mussel flesh in summer 1965 (not shown in the tables) over a period of 59 days was 34.0 g ash-free dry weight, in summer 1966 over a period of 24 days also 34.0 g (Table 5). For nr. 66-2 (not shown in the tables) the quantities were 30.8 g in summer 1966 over a period of 35 days and 33.2 g in summer 1967 over a period of 97 days.

Weight in captivity of the nine birds varied from 80-94% (mean 88%) of the initial weight at capture. The weight at capture and mean weight in captivity were not correlated ($r = 0.288$; $p > 0.50$). This, however, needs not to be expected; as mentioned the birds were captured on the nests and according to Mercer (1968) breeding weight is not constant. He showed that female Oystercatchers lose 6.5 to 7.5% of their body-weight during the first half of the incubation period, but regain the initial breeding weight during the second half of the incubation period. No data are available on fluctuations of the breeding weight of males.

The figures show for the nine birds that food intake was not positively correlated with the mean weight in captivity ($r = 0.375$; $p > 0.50$), and only slightly with the initial weight at capture ($r = 0.704$; $p < 0.05$).

If we consider the subsample of the data of the nrs. 66-1, 66-2 and 66-3, from which we have the longest series of weighings in captivity, food intake and mean weight in captivity do show a significant correlation ($r = 0.9972$; $p < 0.025$). The relation between food intake (F) and mean weight in captivity (Wc) is represented by the formula $F = 0.1363\ Wc - 28.1085$ (F in grams ash-free dry weight, Wc in grams). The mean weight of these three birds in captivity was 465 g, corresponding with a calculated food intake according to this formula of 35.3 g of Cockle and/or Mussel flesh, or 179.9 kcal/day/bird (accepting 5.1 kcal per gram flesh, ash-free dry weight).

6. COMPARISON OF FOOD INTAKE IN CAPTIVITY AND IN THE FIELD

Data on food intake of free living Oystercatchers in summer have not yet been published. Calculations based on direct field observations in daylight in the months of July and August with Oystercatchers feeding on *Macoma* show 83, 119 and 150 ml fresh flesh/low water period (5 hours)/bird; feeding on *Cardium* 81 and 97 ml (Hulscher, in preparation). When the caloric content of *Macoma* flesh is taken equal to that of *Cardium* (0.98 kcal/ml fresh), the intake was 79-147, mean 104 kcal/low water period/bird. There are 1.93 low water periods per 24 hours. It is as yet reasonable to assume no difference between feeding rates in daylight and in darkness awaiting more reliable figures on food intake at night in the field (cf. page 000 and discussion). In this case the daily intake of free living Oystercatchers in summer must be between 153-283 kcal/bird, with a mean of around 200 kcal/bird. This is about 1.4 times as high as the mean intake of my 9 experimental birds in captivity.

7. DISCUSSION

Drinnan (1958b) and Heppleston (1971) also performed experiments on food intake in daylight and in darkness with captive Oystercatchers offering Mussels as food, available 24 hours per day. Drinnan measured the food intake of two birds over a period of 4-6 days under outdoor conditions in December. No data on temperatures are given. Heppleston experimented with a subadult female bird over a period of 4 weeks in April under controlled indoor conditions with periods of daylight and darkness of 12 h each at a temperature of 13°C. Drinnan found that the feeding rate (over 4 days) from dusk to dawn was about half as high as from dawn to dusk. Heppleston found a feeding rate during the night period 0.58 times that during the light period. A lower feeding rate in darkness compared to that in daylight as found by these authors is in agreement with my findings under comparable conditions, namely, a nightly food intake 0.86 times that during the day (Table 2). Basing himself on the results of his experiments with birds in captivity under a non-tidal schedule, Drinnan postulated that at night in the field under natural tidal schedules Oystercatchers feed at a rate half as high as in daylight. This assumption is not supported by my more extensive experiments with captive birds feeding under a tidal schedule. But we must keep in mind that during my experiments the higher feeding rates shown by the birds around midnight may be influenced by the low feeding rates around midday.

There are no direct field observations available on feeding rates of Oystercatchers feeding upon Mussels at night. One of my experimental birds taken out onto natural Cockle beds showed the same feeding rate in daylight as in darkness (Hulscher, in preparation). A priori there are no reasons to suppose that the feeding circumstances for Oystercatchers feeding on Mussels at night differ in field and in captivity conditions. In both cases the Mussels the birds are feeding upon are aggregated and not covered by water. The behaviour of my birds feeding on Mussels in captivity was the same in daylight and in darkness, as could be observed with infrared binoculars. On opening a Mussel the Oystercatcher starts with visually directing its bill in a special position towards the cleft between the valves. Apparently the faint-light circumstances under the natural night sky are sufficient for this act. On the average the light intensity on the mudflats is somewhat higher than in the cages.

Whether or not the food intake in hours of darkness is lower than in hours of daylight should be verified by direct field observations. Perhaps experiments with captive birds feeding under a schedule precisely corresponding with that of the natural tide (*i.e.* becoming progressively later every day) may help to settle this point.

The mean daily food intake of the single Oystercatcher of Heppleston over the 4 weeks was 148.5 kcal; the body-weight remained constant at about 420 g. Taking my formula $F = 0.1363Wc - 28.1085$ a bird of 420 g would consume food to a value of 148.6 kcal in summer (1 g ash-free dry weight of Mussel flesh 5.1 kcal; Heppleston found 5.385 kcal for April). The mean daily intake of the birds of Drinnan over a period of 6 days was 237.6 ml fresh Mussel flesh (63.5 g dry weight ash included) for one bird with a constant body-weight of about 452 g, and 257.3 ml fresh (68.7 g dry weight ash included) for the other with a mean body-weight of 472 g. The ash content and the caloric value of the Mussel flesh is not given. If we use a mean figure for the ash content of 10% and for the caloric content 5.1 kcal per gram ash-free dry weight, then the daily intake of these two birds was 291 and 315 kcal, respectively. Calculated with my formula Oystercatchers with corresponding body-weights would take in summer 170.8 and 184.7 kcal per day, respectively, so that the intake in winter would be about 1.7 times as high as in summer. This seems plausible but it must be remarked (see Fig. 2) that a sample of only 6 consecutive days to measure average food intake might not be fully representative. Further observations on winter uptake are thus urgently required.

When comparing the energy requirements of different birds under different conditions it is convenient to report the energy intake in relation to the energy expenditure under standard metabolic conditions. Standard metabolism can be calculated with a formula provided by King and Farner (1961)*). As we have seen, the mean intake of my three birds 66-1, 66-2 and 66-3 in captivity was 179.9 kcal/24 h/bird, with a mean body-weight of 465 g. This body weight corresponds with a calculated standard metabolism of 42 kcal/24 h. The mean energy intake of these three birds in captivity in summer therefore was 4.3 times the standard metabolism. Quantitative data on the energy intake of waders in captivity have not been published. According to Siegfried (1969) the gross energy intake of the Cattle Egret *Ardeola ibis* in captivity was 3 times as high as the standard metabolism, that of the piscivorous Wood Stork *Mycteria americana,* also in captivity, was 2.7 times the standard metabolism (Kahl 1964).

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9. SUMMARY

Feeding experiments in captivity were carried out in the summer of 1964 to 1967 with Oystercatchers caught on their nests on the island of Schiermonnikoog in the Dutch Waddensea. The birds were fed with Cockles and/or Mussels.

When food was available 24 h/day (non-tidal schedule), the feeding rate (ml Mussel flesh/h) was not constant. Although there were large differences between individuals (Fig. 1A), the feeding rate during darkness was generally only slightly below the average daylight figure (0.86).

*) $\log M = \log 74.3 + 0.744 \log W \pm 0.074$; M in kcal/24 h, W in kg.

When food was available 5 or 7½ hours around midday and again 5 or 7½ hours around midnight (tidal schedule), the mean feeding rate at night of the three birds tested was 1.45 times as high as that during the day.

The daily food intake was independent of the size of the Mussels the birds were feeding upon, all of which were within the range normally taken (Table 3).

The daily food intake showed no difference if the birds had 2 × 5, 2 × 7½ or 24 hours available for feeding per day (Table 4). The daily food intake of individuals varied between wide limits, but over longer periods the daily caloric consumption was about constant, while the birds roughly maintained constant body-weight irrespective of whether they were taking *Mytilus* or *Cardium* as food source.

For a sample of nine birds food intake was measured over long periods. The mean intake of these nine birds varied from 23.5—36.3 (mean 28.8) g Mussel and/or Cockle flesh (ash-free dry weight) per day (Table 6), corresponding with 120—185 (mean 147) kcal/24 h/bird. For a sample of three birds (out of the nine mentioned above), for which a great number of weighings are available, the food intake (F, in kcal/24 h) and the mean body-weight in captivity (Wc, in grams) were correlated ($F = 0.1363Wc - 28.1085$). The gross energy consumption in captivity is 4.3 times as high as the calculated standard metabolic rate.

10. REFERENCES

Dare, P. J. & A. J. Mercer, 1973. Foods of the Oystercatcher in Morecambe Bay, Lancashire. Bird Study 20: 173–184.

Davidson, P. E. 1967. A study of the Oystercatcher (*Haematopus ostralegus* L.) in relation to the fishery for cockles (*Cardium edule* L.) in the Burry Inlet, South Wales. Fishery Invest., London, Ser. II, 25 (No. 7) 28 pp.

Dewar, J. M. 1908. Notes on the Oystercatcher (*Haematopus ostralegus*) with reference to its habit of feeding upon the mussel (*Mytilus edulis*). Zoologist 12: 201–212.

Drinnan, R. E. 1957. The winter feeding of the oystercatcher (*Haematopus ostralegus*) on the edible cockle (*Cardium edule*). J. Anim. Ecol. 26: 441–469.

———, 1958a. The winter feeding of the oystercatcher (*Haematopus ostralegus*) on the edible mussel (*Mytilus edulis*) in the Conway Estuary, North Wales. Fishery Invest., London, Ser. II, 22 (No. 4) 15 pp.

———, 1958b. Observations on the feeding of the oystercatcher in captivity. Brit. Birds 51: 139–149.

Heppleston, P. B. 1971. The feeding ecology of oystercatchers (*Haematopus ostralegus* L.) in winter in northern Scotland. J. Anim. Ecol. 40: 651–672.

Hughes, R. N. 1970. An energy budget for a tidal-flat population of the bivalve *Scrobicularia plana* (Da Costa). J. Anim. Ecol. 39: 357–381.

Kahl, M. P. 1964. Food ecology of the Wood Stork (*Mycteria americana*) in Florida. Ecol. Monog. 34: 97–117.

King, J. F. & D. S. Farner, 1961. Energy metabolism, thermoregulation and body temperature. In: A. J. Marshall (ed.). Biology and Comparative Physiology of Birds. Vol. 2, p. 215–288. Academic Press, New York-London.

Mercer, A. J. 1968. Individual weight change in breeding Oystercatchers. Bird Study 15: 93–98.

Siegfried, W. R. 1969. Energy metabolism of the cattle egret. Zoologica Africana 4: 265–273.

11. SAMENVATTING

De voedseloecologie van de Scholekster is voor verschillende onderzoekers onderwerp van studie geweest. Er zijn reeds vele veldwaarnemingen verricht over de hoeveelheden voedsel die Scholeksters overdag opnemen. Gegevens over de voedselopname 's nachts zijn echter nog onvoldoende.

Door de voedselopname van Scholeksters in gevangenschap nauwkeurig te bestuderen, zowel overdag als 's nachts, kan wel een beter inzicht verkregen worden in de totale hoeveelheid opgenomen voedsel per etmaal.

Op Schiermonnikoog werden vogels op het nest gevangen. Zij werden aan één vleugel gekortwiekt en in kooien op een grasveld bij het biologisch veldstation van de R.U. Groningen gevangen gehouden, waarin ook de proeven werden gedaan. De kooien (400 × 400 × 75 cm) waren van kippegaas opgetrokken, zonder dak, met aan de binnenzijde groengekleurde vitrage om te verhinderen dat de vogels hun snavel door het gaas zouden steken en verwondingen zouden oplopen. Een schutting schermde de kooien af van het veldstation.

In het hier beschreven onderzoek zijn de volgende aspecten van kwantitatieve voedselopname bij Scholeksters in gevangenschap bestudeerd:

— voedselopname als het voedsel 24 uur beschikbaar was,

— voedselopname onder nagebootste getijomstandigheden,

— voedselopname overdag en 's nachts,

— voedselopname met verschillende soorten prooidieren (Kokkels en Mossels),

— voedselopname in verband met lichaamsgewicht.

Wanneer het voedsel 24 uur per etmaal beschikbaar was (getij-omstandigheden uitgeschakeld), dan bleek de snelheid van voedselopname (ml mosselvlees/uur) niet constant te zijn. Er waren grote verschillen tussen de proefdieren onderling (Fig. 1A), maar algemeen was de snelheid van voedselopname 's nachts slechts weinig lager dan overdag (0,86).

Wanneer voedsel gedurende 5 of 7½ uur rond de middag en weer gedurende 5 of 7½ uur rond middernacht (getij-schema) beschikbaar was, bleek de gemiddelde voedselopname in de nachtelijke periode bij de drie gebruikte proefdieren 1,45 maal zo hoog te zijn als overdag.

De gemiddelde voedselopname per etmaal was onafhankelijk van de grootte van de aangeboden Mossels, die alle binnen de afmetingen vielen die ook in het veld genomen worden (Tabel 3).

De gemiddelde voedselopname per etmaal vertoonde ook geen verschillen of de vogels nu gedurende 2 × 5, 2 × 7½ of 24 uur voedsel ter beschikking hadden.

De voedselopname van individuele vogels schommelde sterk van dag op dag, maar over langere perioden was de dagelijkse consumptie aan calorieën ongeveer constant, of de vogels nu Mossels of Kokkels aten (Fig. 2). Hierbij bleef het lichaamsgewicht vrij constant. Voor negen vogels varieerde de gemiddelde opname van 23,5–36,3 (gem. 28,8) g mossel- en/of kokkelvlees (asvrij-drooggewicht)/24 uur (Tabel 6), of 120–185 (gem. 147) kcal/24 uur/vogel. Voor drie vogels, die vele malen gewogen werden, waren de voedselopname (F, in kcal/24 uur) en het gemiddelde lichaamsgewicht in gevangenschap (Wc, in grammen) met elkaar positief gecorreleerd ($F = 0{,}1363Wc–28{,}1085$). De hoeveelheid opgenomen energie in gevangenschap was 4,3 maal zo hoog als het berekende energieverbruik onder standaard metabolische omstandigheden.

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